Climatic Effects on Survival and Reproduction of the Desert Tortoise (*Gopherus agassizii*) in the Maricopa Mountains, Arizona

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TABLE OF CONTENTS

ABSTRACT

The desert tortoise (*Gopherus agassizii*) population at the Maricopa Mountains, Maricopa Co., Arizona, had the largest desert tortoise population collapse known in the Sonoran Desert. The population has declined from over 140 to approximately 20 from 1987 to 1994. An unusual eight year drought, detected by the Palmer Drought Severity Index (PDSI), coincided with the period when the tortoises died. The correlation of annual mortality and summer PDSI is significant. Mortality occurred disproportionately on the hotter, drier, and less vegetated S and SW exposures, while tortoises in the Maricopa Mts. preferentially utilized N and NE slopes. Ecological correlates including high sahuaro mortality and changes in other indicator species during the study support the climate hypothesis. Adult tortoises, especially females, were the hardest hit by the environmental stresses. Tortoises with high domed shells also suffered higher mortality than flatter shelled tortoises during the drought at the Maricopa Mts. The diet was composed mostly of woody perennials, in contrast to other Arizona populations, which have higher quantities of succulent and energy-rich annual plants in the diet.

Reproduction was investigated to assess drought effects on the potential for population recovery. Ovulation in the Maricopas started on approximately June 5 and oviposition was completed by July 24, in 1994. The number of females reproducing at the site of population collapse was significantly lower than at a nearby control site (Espanto Mt.) without high mortality. At Espanto, environmental stressors appeared less severe. Other than proportion of females reproducing, fecundity of the Maricopa and Espanto females was comparable to previously studied Sonoran tortoise populations. Clutch size increases with carapace size for *G. agassizii* and *G. berlandieri.* Body weight gradually declined during the arid premonsoon reproductive season, then dropped substantially at oviposition, and was quickly restored after heavy precipitation. The population of desert tortoises in the Maricopa Mts. may recover, assuming a return to climatic normalcy, but recovery will be slow due to the apparently low reproductive rate of desert tortoises in the Sonoran Desert.

INTRODUCTION

The desert tortoise population at the Maricopa Mountains has recently suffered the largest known decline of any Sonoran Desert tortoise population. The present study was initiated to gain insight into desert tortoise mortality and reproduction under these circumstances, as well as to assess the status and future of the Maricopa population.

Baseline data on desert tortoises were collected at the Maricopa Mts. in the spring and summer of 1987 by the Bureau of Land Management (BLM; Wirt 1988); 57 live tortoises were registered and 65 shell remains were found. Arizona Game and Fish Department (AGFD) recensed the plot in 1990 (Shields et al. 1990) under the Arizona Heritage Desert Tortoise Monitoring Program. They found only 17 live tortoises, but 54 dead ones (15 marked from 1987, 39 unmarked but mostly recently dead). The following year, AGFD conducted a disease survey in the Maricopas (Hart 1992), yielding two more remains in the plot and nine more in locations around the Maricopas, suggesting that the mortality had not been restricted to the plot.

Drought was initially suspected as the cause of desert tortoise mortality on the Maricopa plot, but findings were considered inconclusive (Shields et al. 1990). Recent physiological data from drought periods in the Mohave Desert (Peterson 1993; Henen 1994), and further review of mortality correlates in the Maricopas (Wirt 1995) reinforced the idea that drought lies at the root of the mortality.

Drought conditions are most likely to develop from accumulated moisture deficits over several months or more. Environmental conditions deteriorate as soil moisture is lost, which implicates both soil type and temperature in drought severity. The Palmer Drought Severity Index (PDSI; Palmer 1965) incorporates precipitation, potential and actual evapotranspiration, infiltration of water into the soil zone, and runoff for six months prior to a given date, with the last two months weighted more heavily than the previous four months. The duration and severity of aridity is expressed as a negative or positive PDSI value and is relative to the long term average. A negative value indicates dry conditions. PDSI is used at the University of Arizona for interpretation of long term environmental changes, including for drought histories in the West using pine tree-rings (Stockton and Meko 1975) and mortality of sahuaro and creosote in the Sonoran Desert (Goldberg and Turner 1986; Turner 1990).

The time period from the mid 1980s through the early 1990s was super hot, with record high summer temperatures and record numbers of days over 100° F (37.8°C) in Phoenix and Tucson. And Gila Bend, adjacent to the Maricopa Mt. bajada, was the reported "Hot Spot of the Nation" on television news weather programs several summers in a row during this period. Summer monsoons were late the and rains were generally disappointing. The extreme temperatures of this period, in combination with annually or seasonally low, and late summer rainfall, were the key to the drought effects demonstrated by the PDSI for the Maricopa region.

Site Descriptions

Maricopa Mountains. The Maricopa Mts. are located in Maricopa County between the Sierra Estrellas and Gila Bend (Fig. 1). They are low mountains, but extend over a large area. Vegetation is typical of the palo verde-sahuaro association in the Arizona Upland Subdivision of the Sonoran Desert, in the Lower Sonoran Life Zone (Brown et al. 1979). The Maricopas lie in the more xeric, western edge of this Subdivision. The Little Rainbow Valley on the north and east side of the Maricopas is dominated by creosote flats, with large washes dominated by ironwood, blue palo verde, and mesquite. To the west lies Gila Bend, on the Gila River, at the upper end of the lower Gila Valley. This is lower than the Little Rainbow Valley, although both are representative of the true desert of the Lower Colorado Valley Subdivision: a dryer, hotter Subdivision of Sonoran Desert. The region has a history of Native American occupation, cattle grazing, waste disposal, mining, hunting, and off road vehicle recreation and is about 35 miles from downtown Phoenix.

The Maricopa desert tortoise permanent study plot (PSP) is situated on federal land and was established by BLM in 1986. It is composed of four adjacent quarter sections (T4S R2W Sec. 17,18,19, 20), forming a square mile plot in the northern part of the Maricopa Mts. The physiognomy of the plot comprises upper bajada, and a long low mountain ridge running NW-SE cut by narrow washes (Fig. 2). Large granitic boulders and rocky outcrops dominate the landscape.

Espanto Mountain. Espanto Mountain is a narrow, 3 km long, isolated rocky ridge on the east side of the Maricopa Mts, 12 kilometers east of the PSP (T4S R1W, Parts of Sec. 2, 11, 12, 13, 14; Fig 3). Espanto Mt. was selected for the reproduction study because tortoises appeared to be abundant. It later served as the control site for comparative purposes because there was no evidence of large scale mortality.

METHODS

The BLM, concerned about the impact of study on PSP animals, requested that females from the Maricopa plot would not be used for the reproduction study unless necessary. Therefore, tortoises from three localities were used in this study. We studied three marked female tortoises on the plot and two females that lived adjacent to the plot. One additional female was studied in the south end of the main Maricopa Mountain range, six kilometers south of the PSP (Fig 3). Nine females were studied at Espanto Mountain.

Processing Tortoise Captures

Tortoises were found by searching suitable habitat and looking in burrows. When a tortoise was found, it was removed from the shelter site by hand or with the assistance of a blunt tortoise hook if necessary. They were processed in the coolest available location. Data were recorded on a data form, including date, time, location, recorder, tortoise sex, and ID number. Activity was recorded, and habitat parameters collected included sky conditions, temperature profile, elevation, aspect, slope, vegetation, and shelter type. Each tortoise was weighed (in grams) using a strap secured around the tortoise and a spring scale. Pottery calipers and a metric tape were used to make shell measurements on maximum carapace length (MCL), width of the carapace (at the 3rd, 4th, 6th marginals, suture at the 7th-8th marginals, and maximum width), height (HT), plastron length at the gular notch (PLN) and plastron length at the gular tips (PLT) (Berry 1984). Tortoises were marked according to a standard marking code (Ernst 1974) by notching the shell marginals with a triangular file or hacksaw blade. Freshly cut notches were treated with betadine, a topical antiseptic.

1993 Census

Square mile tortoise plots (Berry 1984) traditionally use a 10X10 grid system, with each grid measuring 0.1 miles on a side. Wirt (1988) used a 10X10 grid system beginning with 00 in the northwest corner despite the fact that the plot was composed of four quarter sections. Shields et al. (1990) alternatively assigned the northwest corner to grid 55, and we adopted the latter method for the present study because it facilitated the incorporation of adjacent areas. The total grid area we searched off-plot was quantified by placing a plastic overlay with a 0.1 mile grid pattern on the appropriate 1:24,000 topographic map and counting each grid of which more than half the area was searched.

In 1993 we covered 38 out of 100 grids (approximately 1.0 km^2) on the Maricopa PSP (Fig 2). We worked 17 calendar days and 40 total person days conducting this survey, during which the area was covered once thoroughly. In addition, we repeatedly searched areas of the PSP where recent tortoise sign was found in order to locate females for the reproduction study. Areas adjacent to the PSP, as well as the South End and Espanto Mountain were searched first to obtain females for the reproduction study. Total field effort in 1993 was 30 calendar days, 94 person days, and 155 grids covered. The average search time was 7.1 hours per person-day in 1993.

Processing Tortoise Shells

More than 140 desert tortoise shell remains were collected from the Maricopa Mts. between 1987 and 1995. Shells were numbered dated, measured and cataloged. Some remains had portions missing due to predators or scavengers, and measurements were taken on the available material. To estimate time since death (TSD), they were sorted by degree of weathering; remains consisting of separated, old, assemblages of bones were not assessed. Remains were sorted into the following four categories; (1) shell with firm articulation and scutes firmly attached, (2) scutes loosened and/or some missing, and the exposed bone smooth without signs of weathering, (3) scutes more than 50% loosened, and/or missing, cracks and/or pitting in the bone and/or separation between the bone sutures, (4) shell integrity weak, and definite signs of bone weathering including large cracks, bone pitting, or suture separation, no organic material remaining inside the shell, black or pink fungus present. Time since death was assigned as 0-3 yrs respectively, and then the year of death was computed by subtraction from the year of collection. The basis for translating shell deterioration into TSD was derived from the 1990 and 1993 shell sample, which included 23 marked animals that provided a reference for maximum time since death.

Climatic Analysis

Climate data came from two sources. We collected our own precipitation data with plastic rain gauges with mineral oil to prevent evaporation at the three study areas, and we collected temperature data with max-min thermometers. These data were recorded during each site visit throughout the census and reproduction studies.

For more continuous precipitation and temperature data, we obtained climatic records from the Arizona State Climatologist (National Oceanic and Atmospheric Administration; NOAA) for Buckeye, Arizona (1965-1993). PDSI has been made available by NOAA for operational use (Karl 1983) and slightly modified for analysis of local climates by the Laboratory of Tree-Ring Research at the University of Arizona.

Rephotography

Photographs taken in 1987 demonstrating tortoise habitat in the PSP were made into 8x10 prints. Photo points for the 1987 photos were relocated, rephotographed in 1995 and also made into prints. Table 1 summarizes photograph locations in the PSP. The prints were photocopied and a highlighting marker was used to partition the foreground according to slope and to mark features for comparison between years. Although we had intended to compare vegetation cover between the photos, sahuaros were the most measurable feature in the photographs. They were counted by slope aspect, and were compared for presence or absence between photos.

Vegetation Transects

Over the years, perennial and ephemeral vegetation has been sampled at 14 sites on the Maricopa PSP. Six line-intercept transects were done in 1995 to provide additional data for this project. Three types of vegetation sampling (of different sizes) were used at the Maricopa PSP. These include a belt transect that describes an area of vegetation (Strong 1966); line-intercept transects (Greig-Smith 1983); and quadrats to describe annual vegetation (Greig-Smith 1983). Additionaly, two large rectangular quadrats were sampled for riparian perennial vegetation. Herein, frequency is the number of transects and/or quadrats in which the species was observed; relative frequency is the same number divided by the total for all species, X 100.

Diet

We used two methods with scat as the primary source of diet information. Tortoise fecal pellets collected on the PSP were sorted under a dissecting microscope for seeds, florets, nutletts, or any other diagnostic plant fragments. Seventy-nine samples were sorted and examined. Frequency tables for tortoise diets were constructed from the plant lists for each scat. We express diet preference simply as relative frequency in the diet (among scat samples) minus relative frequency in the environment (among vegetation transects and quadrats) for each plant species. It is the least biased and most robust measure given the small sample sizes available.

Several scat samples were sent to the Range and Fecal Analysis Lab at the University of Arizona for microhistological analysis (Hansen et al. no date) to quantify percentages of the main components of the tortoise diets. In this analysis, the sample is finely ground up and made into a slurry. Four slides are made and the samples are read by an analyst who is able to recognize the plants from their cuticles. A set number of "fields" is read from each slide. Percent frequency (F) of paticles per location is then converted to density (D) from a table based on the formula

$$F = 100(1 - e^{-D}).$$

Telemetry

Telemetry was used to locate tortoises for X-raying and body mass monitoring in the reproduction study. Telonics (Mesa, AZ) telemetry units including a TR-2 receiver, Yagi antennae and CHP-4P transmitters, were used. Transmitters were attached to the lower half of the 3rd and 4th costal scutes of the tortoise's shell using Devcon 5-minute epoxy gel. The antenna was epoxied around the dome of the shell, gapping the suture between scutes to avoid causing growth disorders.

Table 1. List of areas photographed in 1987 and in 1995 at Maricopa desert tortoise study plot, Maricopa Co., AZ.

Photo	Sec/grid	View
1	18/57	W
2	18/66	W
3	18/95	SSE
4	18/95	ESE
5	19/52	SSE
6	19/38	NNE
7	19/38	NE
8	19/38	E
9	19/38	ESE
10	19/38	N
11	19/07	SSW
12	19/07	SW
13	18/87	NE
14	18/98	NW
15	18/98	E

Radiography

Methodology for the reproductive study was modified from Turner (1986), as in Murray et al. (1996) for Mazatzal Mountains, Arizona. The use of X-rays for collecting reproductive data on turtles (Gibbons and Green 1979) is nonlethal and does not detectably damage the female or embryos. Tortoises were brought to the vehicle, where a portable MinXray 210 X-ray machine (on loan from the University of Arizona's Department of Animal Care and Department of Animal Sciences) was suspended from a modified tripod. The X-ray machine was powered with a Honda 250 generator. The tripod was adjusted to suspend the X-ray condenser 28 inches from the ground surface. Kodak X-Omatic Lanex™ regular screen cassettes (24 x 24 cm) were placed on the ground under the condenser, and tortoises were placed on the cassettes for 0.3 second exposures of Super HR-G Fuji X-ray film at 13 mA and 63 kV peak. X-rays were transported back to Tucson in a cooler with blue ice and developed in a Fuji 9000 automated processor at the Radiology Department in the University of Arizona's Medical Center.

We made trips approximately every 5-12 days to the Maricopas to X-ray tortoises, beginning in early May and extending through July 1994. Because the study areas were several hours apart, and it was critical to move tortoises during the coolest hours, a staggered schedule was used. Tortoises were taken out of their burrows and carried back to the vehicle in clean sacks. It was essential to keep the tortoises as cool as possible at all times by working in the early morning hours and wetting the bags when it became warmer. After X-raying, the tortoises were weighed and returned to their burrows, again taking care to avoid exposing them to high temperatures. After oviposition, Espanto tortoises were monitored for movements and mass changes to watch for any indication of second clutches, but they were not X-rayed. In 1995, two X-ray trips were made to gather supplementary reproductive information on Espanto females that retained their radio transmitters.

Soils

Nest sites were confirmed in two ways. Several females demonstrated nest defense (Murray et al. 1996) by occupying burrows after oviposition, including after rains, at times when other tortoises were generally making large movements. Nest sites were also confirmed when we found concentrations of eggshell fragments on the ground or in burrows, although we were unable to determine which tortoise had laid the eggs. Soil samples were collected from nests in the spring of 1995. The samples were sifted through a 1 mm USGS sieve to quantify gravel content. Soils were described for texture (Miller et al. 1951), structure (Soil Survey Staff 1951), and color (Munsel Color Co. 1965). For comparison, soil samples were collected from vegetation transects and random locations.

Statistical Analyses

Contingency tests were performed manually and critical values were obtained from Iman and Conover (1983). Descriptive statistics, t tests, and regressions were calculated using Excel® version 5 for the MacIntosh computer (Microsoft Corporation 1993). Principal components analyses (PCA) were performed with SAS® version 6.03 for the PC (SAS Institute 1988).

We used PCA to examine variation in shell shape between surviving and non-surviving tortoises based on log-transformed measurements of length (MCL), width (M7/8), height

(HT), and plastron length (PLT). Log-transformed variables were regressed on the first principal component and the residuals were separated according to sex. After the values were ranked, both sexes were combined and then the values were partitioned into survivors and non-survivors. The two groups were compared using a Wilcoxon-Mann-Whitney rank sum test. This procedure provided the means to remove the effects of size, allometry, and sex.

RESULTS

Climatic Conditions and Environmental Correlates

Drought. Climatic conditions in the Maricopa Mts. estimated from the PDSI values for Buckeye are shown in Figure 4. The 28 year period from 1956-1978 fluctuated between moderately wet and dry years as expected for a desert climate, slightly favoring wet years over dry. Minor droughts occurred in 1964-1966, and 1969-1970. A serious 1979-1980 drought in the Maricopa region was broken by an enormous rainfall event (108.5 mm) in August 1982, with wet conditions persisting well into 1983. This event, with good summer and winter rains in tandem, was the wettest period during the lives of the Maricopa tortoises. The effects of this rainfall pattern undoubtedly improved habitat conditions created by the 1979-1980 drought. Drought returned to the area by September 1983, and a series of three poor summers followed. Good conditions occurred briefly in February and March 1985 and 1986, but drought reigned each summer until 1987, resuming January 1988 through May 1992. This remarkably dry eight year period, September 1983 to May 1992, had favorable spring conditions just twice and favorable summer conditions just once during its duration.

Mortality of sahuaros. Estimates of environmental conditions are supported by quantitative changes and noted observations of the Maricopa Mts. biotic communities. Additional environmental evidence was demonstrated by fifteen photographs taken in 1987 and retaken in 1995. These provide an opportunity to view a variety of correlated effects of climatic stress in the study area. The most noticeable difference is the absence or death of sahuaro cacti.

Differences in sahuaro mortality rates between different aspect slopes provide striking evidence that climatic stress was present in the Maricopas during our study period. The percent mortality on S to WNW facing rock slopes was greater than on NW to SSE aspect rock slopes or on bajadas (Tables 2 and 3). This is most likely a reflection of the rule that southerly and westerly exposures are hotter and drier while northerly exposures are less hot and not so arid.

Observed changes in flora and fauna. Many organisms besides desert tortoises and sahuaro cacti were affected at the population level by the climatic extremes in the Maricopas. Table 4 lists seven species of plant and animals for which evidence of decline was found and five that appeared to have benefitted once the drought ended, as compared to our observations in Organ Pipe Cactus National Monument and the Tucson Mountains. In general, all animal species appeared to have reduced numbers du ring the drought; however, those with large southwesterly distributions were more abundant orrecovered quickly when the drought ended, presumably because of their adaptation to less predictable summer rainfall. Species showing mortality or reduced numbers without rapid recovery generally had more easterly distributions with summer rainfall activity maxima, and probably began the drought with higher than

Table 2. Sahuaro cactus mortality at sites photographed in 1987 and 1995 on the Maricopa PSP, Maricopa Co., Arizona.

Photo	Sec/grid	View	Situation	Aspect	Dead	Total
1	18/57	W	bajada	W	2	44
2	18/66	W	bajada	W	0	42
3	18/95	SSE	slope	N	0	3
3			arroyo	NE	0	8
3			terrace	WNW	2	2
4	18/95	ESE	arroyo	N	0	1
4			slope	N	0	4
5	19/52	SSE	slope	NE	0	1
6	19/38	NNE	slope	W	0	5
6			arroyo	S	1	8
7	19/38	NE	slope	SW	3	17
8	19/38	E	slope	W	0	8
8			slope	SW	5	42
9	19/38	ESE	arroyo	W	5	9
9			slope	NW	0	2
10	19/38	N	arroyo	S	0	0
11	19/07	SSW	slope	E	0	3
11			slope	NE	0	2
12	19/07	SW	slope	SE	0	4
13	18/87	NE	slope	W	3	32
14	18/98	NW	hill	SE	0	7
15	18/98	E	slope	NW	0	3
15			slope	SW	1	15

Table 3. Summary of sahuaro cactus mortality according to slope aspect at the Maricopa PSP, Maricopa Co., Arizona.

Situation	Dead/total	% mortality
A. All NW to SSE aspect uplands	0/38	0.00
B. All S to WNW aspect uplands	20/138	14.49
C. Bajadas	2/86	2.36

Table 4. Biotic changes in indicator species, hypothesized to be climate-related. Changes are based on a comparison of post-drought (1993-1994) observations to early drought (1987) observations. Mortality is based on the high proportion of remains observed in 1987 compared to other localities. Distribution shown is relative to the study area.

Species	Observation	Relative Distribution
Agave deserti	increased number	southwest
Uta stansburiana	increased number	widespread
Crotalus cerastes	increased number	southwest
Crotalus mitchellii	increased number	southwest
Dipodomys merriami	increased number	widespread
Carnegia gigantea	mortality	southeast
Opuntia chlorotica	reduced number	east
Sonorella sp.	mortality	endemic
Orthoporus ornatus	mortality	east
Urosaurus ornatus	reduced number	east
Crotalus molossus	reduced number	southeast
Crotalus tigris	reduced number	southeast

normal numbers following wet periods in the early 1980s. These changes reflect a shift among indicator taxa from Arizona Upland (thornscrub) to Lower Colorado Valley (true desert) conditions over a short span of ecological time.

Vegetation. Results from the vegetation transects from 1987 to 1995 at the PSP are shown in Table 5 for perennials and Table 6 for annuals. Perennial vegetation did not change significantly from 1990 to 1995 at site 8; the only perennial plot conducted twice. Similarly, there was no systematic difference in vegetation cover revealed by repeat photography. Most perennials apparently were affected slightly or temporarily. On the other hand, annual vegetation showed considerable differences between four different spring sample years at site 10. In 1993, 275 individuals of *Bromus rubens* occupied site 10 whereas, in 1995, 1086 specimens of thirteen species occupied the same plot. None of the three sites sampled for summer annuals in 1990 had as many plants as any of the spring samples. Annual vegetation normally varies sharply in density and variety between years and therefore requires a much larger sample size to establish variation patterns. Also, southern aspects were not sampled, which limits the amount of broad interpretation that can be made from the vegetation analyses.

Effects On Maricopa Desert Tortoises

During the 1993 census of the Maricopa PSP, eleven tortoises were captured; six new captures and five recaptures. Eight tortoise shell remains were found including one from a marked individual. Two of the remains were small juveniles (56, 58 mm MCL), two remains were estimated to have TSD estimates of 3 yrs and were likely to have been missed in 1990, one remain had a TSD estimate of 1-2 yrs, and the marked remain had a TSD estimate of 2-3 yrs. For the last two remains it was difficult to estimate TSD: one was trapped in a rock burrow and buried by packrat litter, and the other consisted of bone pieces from a packrat nest.

In searches adjacent to the plot, three live individuals and 18 unmarked and three marked remains were found (two from the PSP and one marked by AGFD in 1989). Eleven remains were estimated to have died from 1990 to 1993 and 10 before 1990. To date, 23 marked tortoise remains from the Maricopas have been found. At Espanto nine live tortoises were captured and two remains were found.

Population decline. Population decline from 1984 to 1995 is shown in Figure 5. A Lincoln Peterson Index estimate for 1987 is also provided in the figure for comparison. The population estimate for each year is an accumulation function of remains based on year of death plus all tortoises captured and known to have been alive in the previous years interpolated from 1987, 1990, and 1993 data. This necessary interpolation has the effect of smoothing out variation in mortality rates among adjacent years. We estimated mortality rates by dividing the number of shell remains assigned to a year by the estimated population (Fig. 5) for the proceeding year. Less accuracy in the mortality rate estimates is expected for early years because very degraded (generally older) remains were excluded, and for later years because sample sizes are smaller (i.e., according to the law of small numbers).

Drought severity and mortality rate. Mortality rates for each year are compared to the corresponding PDSI (average for June, July, and August) in Figure 6. Linear regression of mortality rate on summer PDSI returns a highly significant correlation; $r=.78$, $N=10$, $P<.01$.

Table 5. Summary of perennial vegetation analyses at Maricopa PSP, Maricopa Mts., Maricopa Co., Arizona. Arranged by habitat situations.

Site	Date	Section	Grid	Size	Method	Situation	Aspect	Species	Density	Diversity*
2	11/14/87	19	38	20X10m	area	arroyo	S	11	$30/100m^2$	6.71
3	11/14/87	19	44, 45, 54	100X25m	area	wash	W	12	$6/100m^2$	4.76
1	4/2/87	19	47	100X2m	area	slope	N	23	$125/100m^2$	9.85
4	11/14/87	19	46	100m	line	slope	N	17	132/100m	7.87
8	10/10/90	18	58, 59	100m	line	slope	N	15	78/100m	9.70
8	4/2/95	18	58, 59	100m	line	slope	N	16	63/100m	8.13
9	10/11/90	17	?	100m	line	slope	?	16	99/100m	9.87
11	2/25/95	18	78	50m	line	slope	NW	14	82/100m	9.90
12	2/25/95	19	7	50m	line	slope	E	11	50/100m	8.62
5	11/14/87	19	36	100m	line	slope	S	11	93/100m	2.13
6	11/14/87	19	54	100m	line	alluvium	W	6	49/100m	2.64
13	2/25/95	19	38	50m	line	alluvium	S	4	22/100m	3.20
14	2/25/95	19	38	50m	line	alluvium	S	4	50/100m	2.96
7	10/10/90	17	50	100m	line	bajada	E	7	25/100m	4.78

Table 6. Summary of annual vegetation analyses at the Maricopa PSP, Maricopa Mts., Maricopa Co., Arizona. Arranged by spring and summer seasons.

Site	Date	Section	Grid	Size	# quads	Situation	Aspect	Species	Density (m^2)	Diversity*
1	4/2/87	19	47	50X20cm	25	slope	N	12	124	5.04
10	4/9/91	18	67	1X1m	1	slope	NW	12	547	3.31
10	4/5/92	18	67	1X1m	1	slope	NW	4	235	1.74
10	4/93	18	67	1X1m	1	slope	NW	1	275	1.00
10	4/1/95	18	67	1X1m	1	slope	NW	13	1086	10.68
7	10/10/90	17	50	50X20cm	10	bajada	E	2	17	1.83
8	10/10/90	18	58, 59	50X20cm	10	slope	N	4	13	2.70
9	10/11/90	?	?	50X20cm	10	slope	?	4	55	2.25

* Diversity $= e^H$ where $H = -\text{sum}\ p_i \ln p_i$ (Shannon-Wiener index); p_i = relative density.

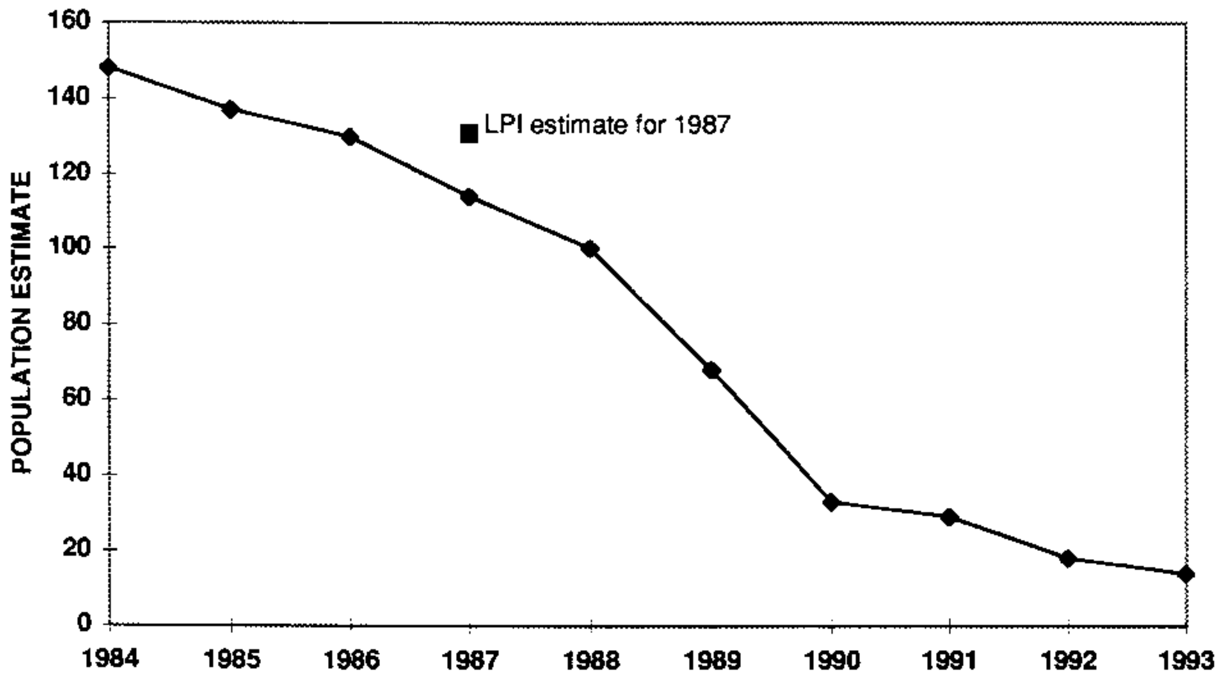

Figure 5. Estimated population decline of desert tortoises at the Maricopa PSP. A Lincoln Peterson Index estimate for 1987 is provided for comparison. See methods for estimation proceedure.

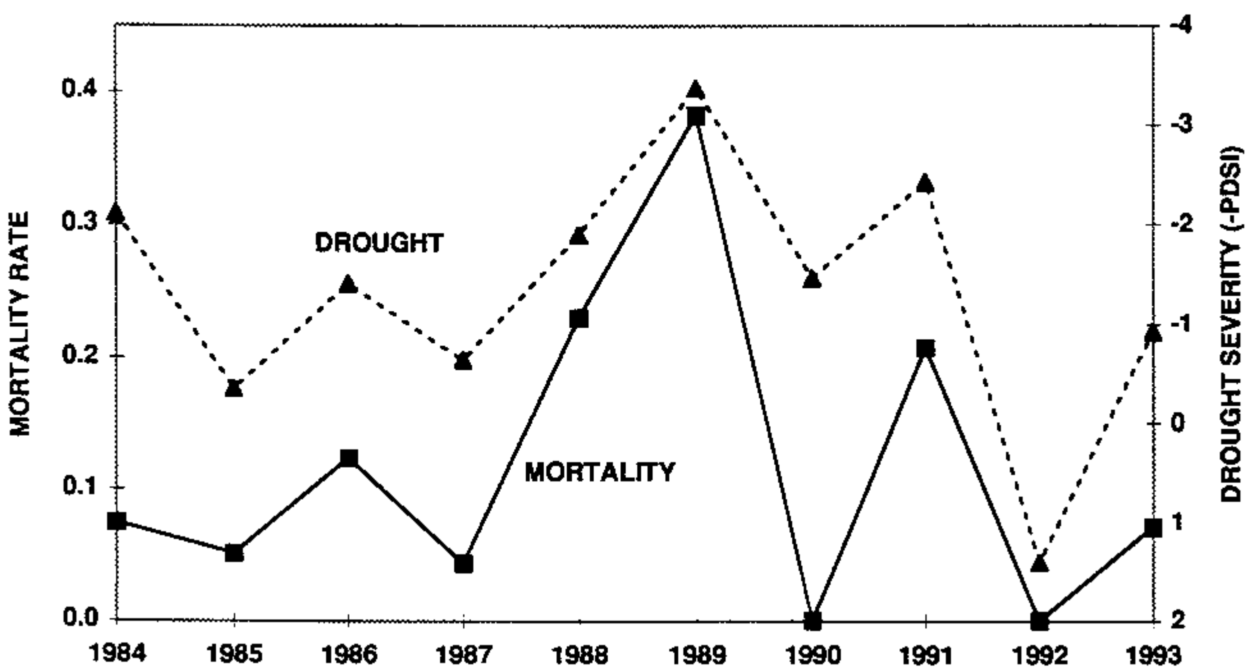

Figure 6. Desert tortoise mortality and summer drought severity (PDSI) at the Maricopa PSP.

Aspect. Figure 7 shows that northerly and easterly aspect slopes had the most turtles during the entire study period, and that survival was heavily skewed toward these less arid slopes that are expected to have less dramatically high maximum temperatures. Our experience in the Tucson Mts. and in Organ Pipe Cactus National Monument suggests that desert tortoises normally utilize all aspects and can achieve high population densities even on southerly to westerly aspect slopes.

Sex ratios. The ratio of sexes among subadult and adult sized remains is 41 males to 64 females or 0.64 to 1. The ratio among live tortoises, those that were never found dead, is 34 males to 19 females or 1.79. The contrast is significant (X^2=8.9, P<.05). These results indicate that females were subjected to a higher mortality rate than were males.

Age and size distributions. Based on the presence of six subadults out of 27 recent live tortoises or "survivors", it appears that subadults may have experienced lower mortality rates than juveniles or adults (Figure 8). Recent live tortoises ("survivors") were seen alive in 1990 or later and were never found dead. However, the sample size is too small for statistical significance despite the large difference in Fig. 8. Among adult-sized turtles, both remains and survivors have nearly the same mean MCL (Figure 9), although again it appears that the smaller adults may have survived better than the larger ones.

Postmortem shell shrinkage. Only intact, marked shell remains were used to obtain measurements to compare live and dead tortoises for shell shrinkage. The remains exhibit an average shrinkage of 3.75% in MCL compared to live measurements (Fig. 10) and a correction factor of 1.0375 was used to adjust remain MCL measurements. Different rates of shrinkage for height and width (Table 7) suggest that sensitive morphometric analyses of shape should not be performed on remains.

Variation in shape. In order to avoid errors due to postmortem deformation of shell shape, we compared the shapes of live individuals that later turned-up dead to those of survivors in 1990 and 1993. We detected a slight but significant difference in residual log height between survivors and non-survivors tortoises even when the effects of size, allometry, and sex were removed (rank transformation test, t=1.966, df=50, P=0.027). This implies selection for lower shells, and hence perhaps for ability to enter a greater variety of shelters, or to get further into them. Sonoran desert tortoises are generally known to be flatter-shelled than Mohave desert tortoises.

Diet. A total of 133 fecal pellets (scats) representing 79 samples removed from the study area or from tortoise remains were examined to gain some insight into diet. The diet at Espanto Mountain was not investigated. At the Maricopa site, 75 plant species were identified in the diet, including 38 perennials, 33 annuals, and four grasses.

The main part of our analysis of tortoise diet was based on fragment analysis and identifying components of scats. Appendix I lists ephemerals and forbs and Appendix II lists perennials found in scats in the fragment analysis along with the relative frequencies from vegetation transects and quadrats.

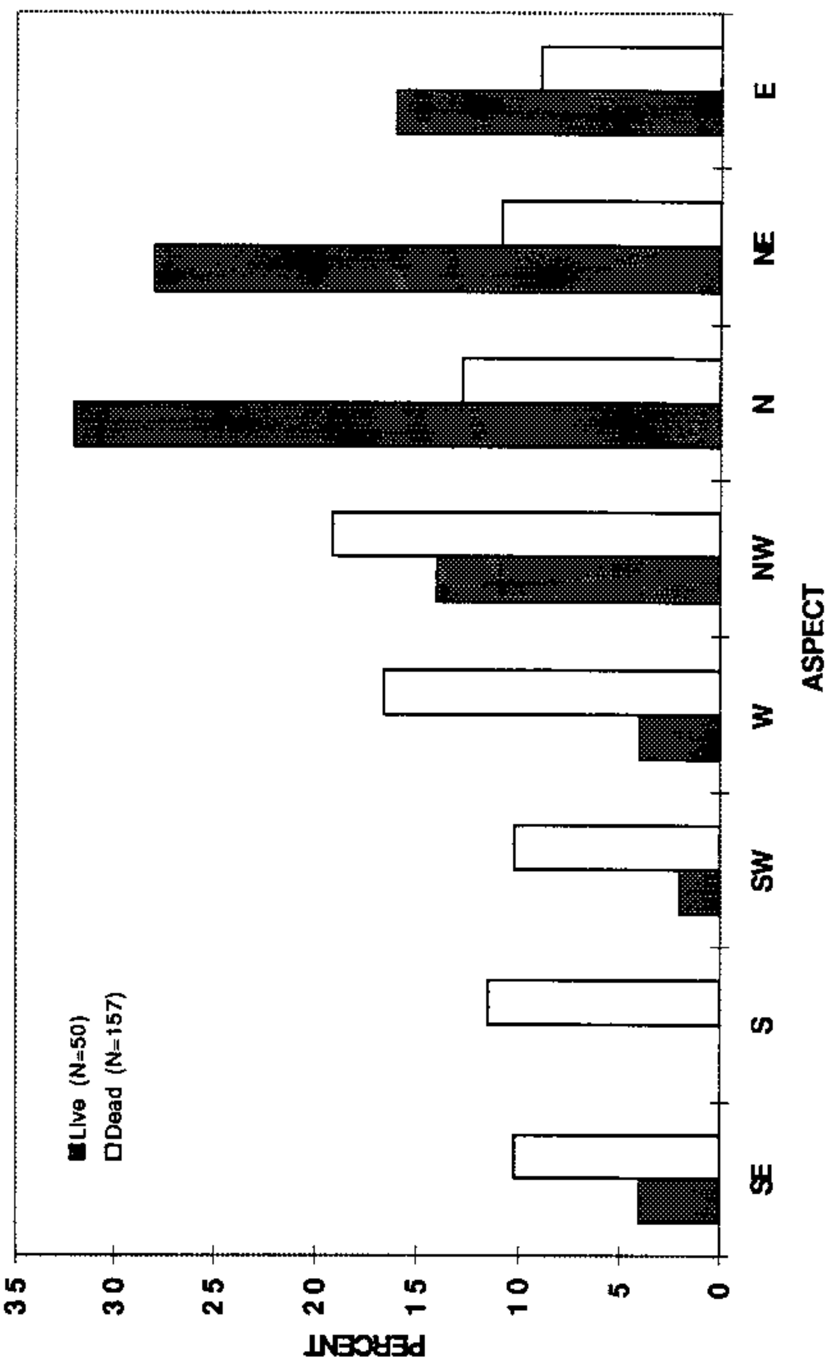

Figure 7. Proportions of live tortoises and remains found on different aspects on different slope aspects in the Maricopa Mountain core, Maricopa Co., Arizona.

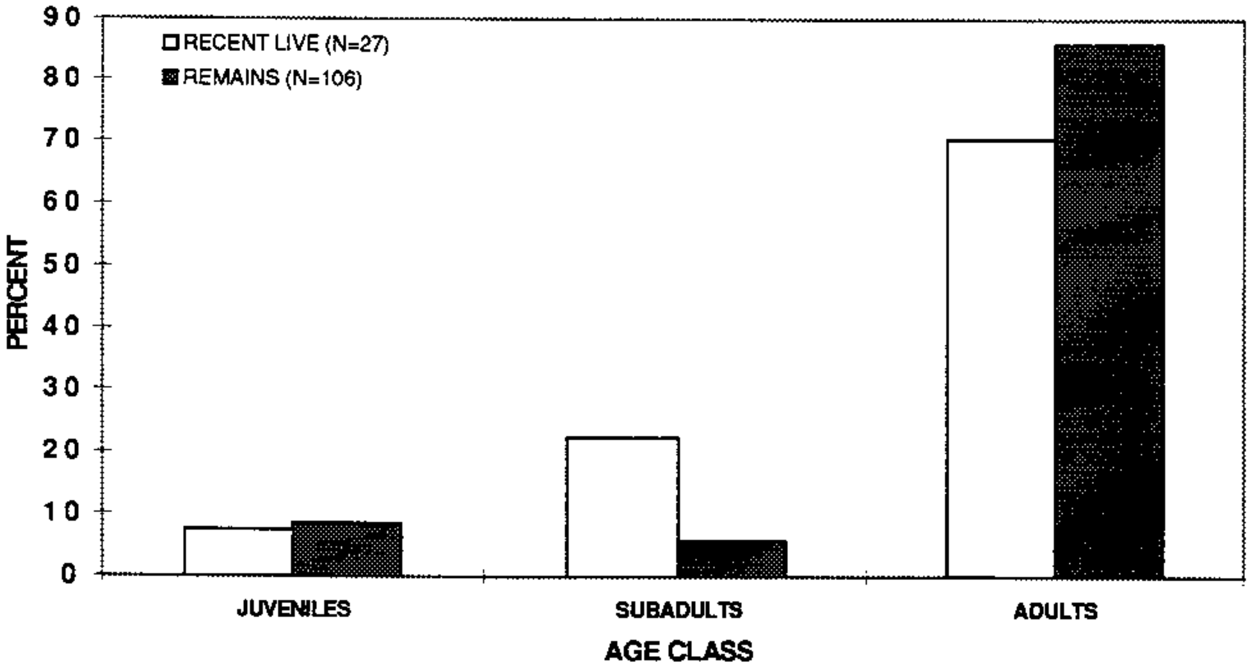

Figure 8. Proportions of juveniles (less than 160mm), subadults (161-210mm), and adults (greater than 210mm) for recent live tortoises and for remains at the Maricopa Mountains core, Maricopa Co., Arizona.

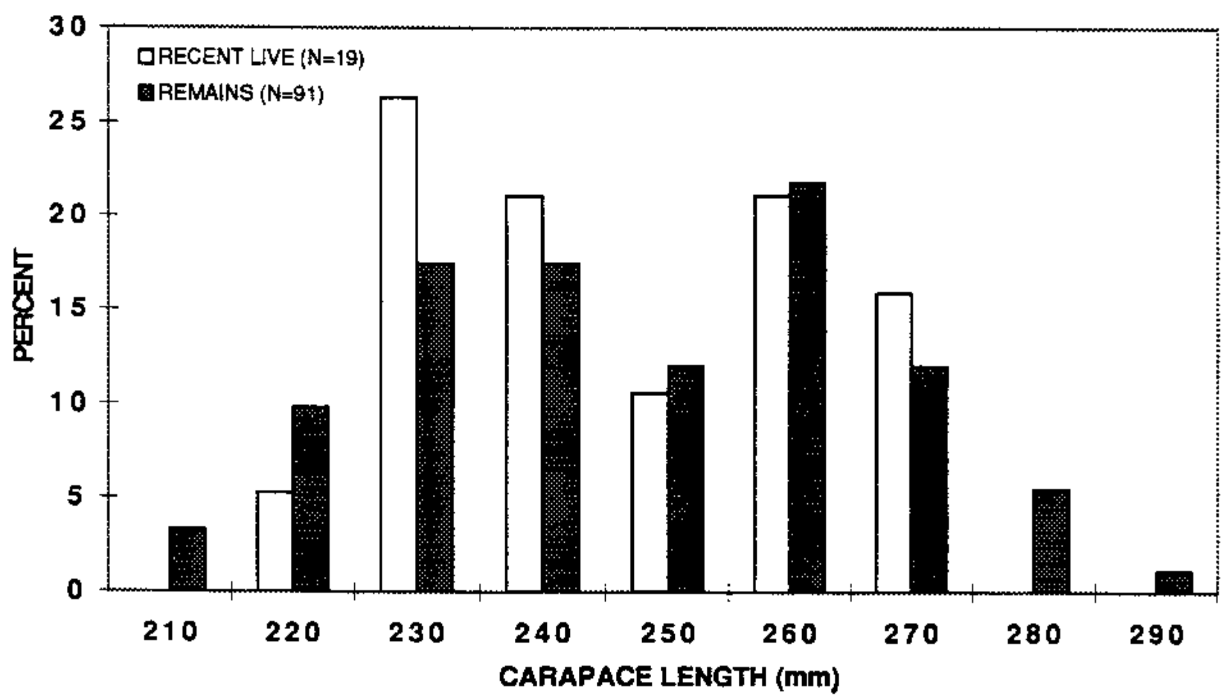

Figure 9. Size distributions of recent live tortoises and of remains found at the Maricopa Mountain core, Maricopa Co., Arizona. Adults only are shown.

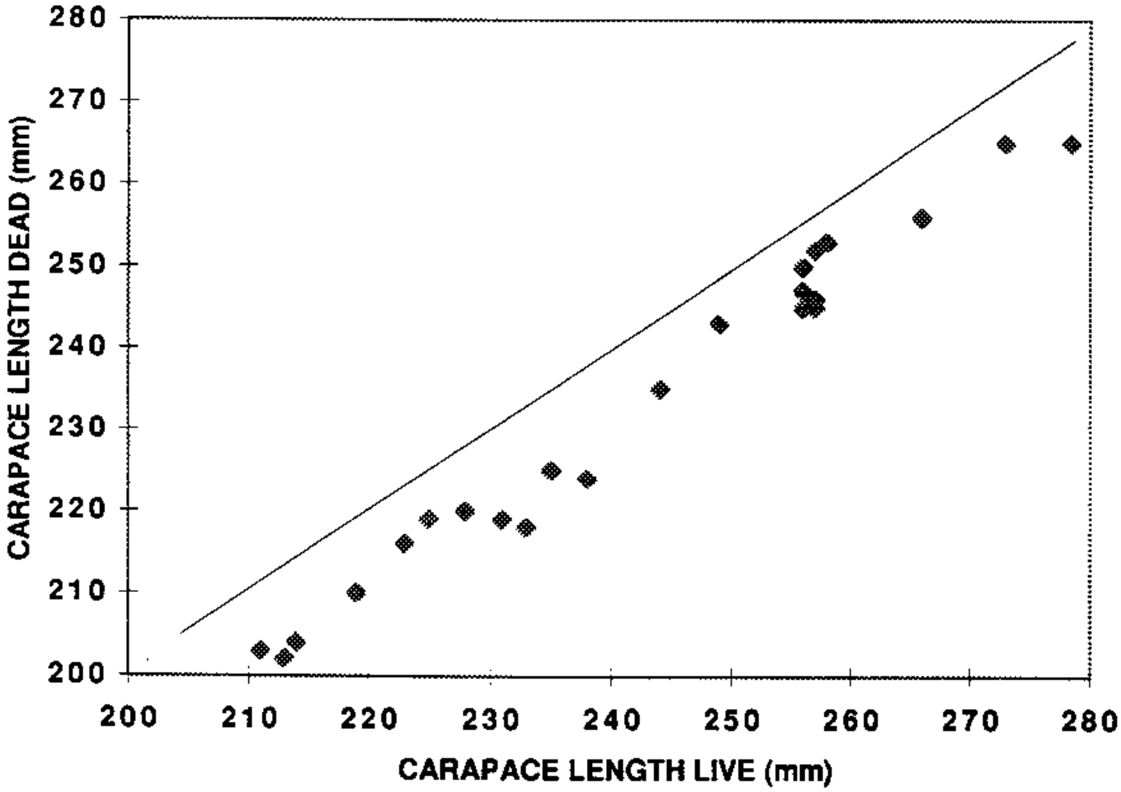

Figure 10. Carapace lengths of remains and of live tortoises (most recent capture). Amount of postmortem shrinkage is the distance below the diagonal line.

Table 7. Comparison of percent shrinkage for length (MCL), width (M7/8), and height (HT) of tortoise shells after death. Percent shrinkage = 100 X (Live - Dead) / Live.

	MCL	M7/8	HT
Mean	3.75	1.99	3.96
Standard Error	0.25	0.36	0.88
Kurtosis	-0.58	2.90	1.02
Skewness	0.25	1.30	0.91
Range	4.50	8.27	17.03
Minimum	1.94	-0.91	-2.25
Maximum	6.44	7.37	14.78
N	25.00	24.00	22.00

We can get a glimpse of species preferences by comparing the frequency of plant species in the diet to that in vegetation transects (Figure 11 and Appendix II). In fact, a regression of frequency in the diet on frequency in the environment produces a highly significant correlation for perennial species (r=.59, N=45, P<.0001). Perennial plants appearing most frequently in the scat samples are *Janusia gracilis, Cercidium microphyllum, Eriogonum fasciculatum, Sphaeralcea ambigua, Dyssodia porophylloides, Olneya tesota,* and *Ditaxis* sp. Frequently observed annuals include *Eucrypta chrysanthemifolia, Lepidium lasiocarpum, Plantago insularis, Bromus rubens,* and *Boerhaavia intermedia.* Some plants appear to be rare or absent in the diet despite being abundant on the plot. These include *Encelia farinosa, Ambrosia deltoidea, Sapium biloculare, Menadora scabra, Viquieria deltoidea, Ephedra* spp., and *Schismus barbatus.*

In order to judge the significance of diet observed from fragment analysis of scats in the Maricopa study, we compared our results to those of Vaughan (1984) for the Picacho Mountains and Hoffmann (1996) for the Mazatzal Mountains (Table 8). Although it would have been ideal to have data from the Maricopas prior to the mortality, the Picacho and Mazatzal studies offered the best available alternatives. The Picacho site was investigated in 1982-1983 during a relatively wet period. The Mazatzal study is part of a current investigation of Sonoran desert tortoise diet funded by the AGFD Heritage Fund.

At the Maricopas, four species with a relative diet frequency greater than five percent were perennials, whereas at the Picacho area, four of five species with greater than five percent relative frequency were annuals. These results suggest that the relative contribution of perennials to the diet of Maricopa tortoises was relatively high.

In addition to fragment analysis, microhistological techniques for analyzing diets of free-ranging livestock were also applied to tortoise diets. This offers the advantage not only of recognizing species that would otherwise have been missed, but it also provides an estimate of relative density (total biomass) of each component in the diet. Seven scat samples from the Maricopa plot were subjected to microhistological analysis. Among the 16 species of plants found in Maricopa tortoise diets, 65% of the mean densities were woody perennials (Table 9).

Additional microhistological material came from the digestive tracts of four shell remains. Of the four animals, two contained perennials and summer annuals, one had perennials and winter annuals, and one had a mixture perennials and both summer and winter annuals. The combined frequencies (N) of perennials compared to annuals and grasses were greater among the four dead animals than among the 75 scat samples from presumably live animals; 28:5 vs 190:178 (X^2=13.469, P<.001).

Reproduction

Reproductive season. Radiography results for the 1994 reproductive season at the Maricopas are shown in Table 10. Oviductal eggs were first observed on June 5-17, and some females are shown to have ovulated between mid-June (June 13-21) and mid-late July (July 13-23). Egg laying was observed for female 133 on July 17, 1994. The minimum number of days the females were gravid was 22-45 days.

Table 8. Comparison of desert tortoise diets at various Arizona sites based on fragment analysis of scats.

	Maricopa	Picacho1	Mazatzal2
	1987-93	1982-3	1996
Season	Mixed	Mixed	April
Samples	78	44	10
Annuals	36.5	41.3	53.7
Grasses	6.8	17.4	20.9
Cacti	3.0	4.4	1.5
Suffrutescent perennials	27.7	20.9	11.9
Woody perennials	27.4	16.0	11.9

1 = Vaughan 1984
2 = Hoffmann 1996

Table 9. Frequencies and mean densities of plant species in the diet based on microhistological analysis of seven scat samples from the Maricopa PSP, Maricopa Co., Arizona.

Form	Species	Freq. N	Mean Dens.
forb	*Eriogonum sp.*	7	0.4143
shrub	*Sphaeralcea sp.*	7	0.3443
tree	*Olneya tesota*	7	0.1514
shrub	*Janusia gracilis*	6	0.4743
cactus	*Opuntia sp.*	6	0.3771
tree	*Cercidium microphyllum*	5	0.1529
ephemeral	*Boraginaceae*	5	0.1414
grass	*Aristida sp.*	4	0.1443
shrub	*Ephedra aspera*	3	0.0357
forb	*Astragalus sp.*	2	0.1000
forb	*Euphorbia sp.*	2	0.0286
grass	*Erioneuron pulchellum*	2	0.0143
shrub	*Lycium berlandieri*	1	0.0314
shrub	*Krameria sp.*	1	0.0314
ephemeral	*Tidestromia lanuginosa*	1	0.0286
shrub	*Hyptis emoryi*	1	0.0114
	TOTALS	60	2.4814

Table 10. Results of radiography of desert tortoises at two sites in the Maricopa Mountains, Maricopa Co., Arizona, 1994. The boxes group a presumed single clutch.

ID	11-May	12-May	13-May	22-May	23-May	24-May	5-Jun	6-Jun	12-Jun	17-Jun	21-Jun	22-Jun	28-Jun	1-Jul	3-Jul	8-Jul	13-Jul	23-Jul
Espanto																		
109							9		9		9			0			0	0
139														6			0	
138														2	0		0	
108			0	0			0		6		6				6		6	0
180																		0
132							F		7		7			7			7	0
133							5				5			5			5	
120			0	0					4		0			0			0	
Plot																		
21	0				0					0			0					
91		0			0					0			0			0		
88					0			4								0		
113	0							0		6						6		
63		0			0							0						
101			0			0			0		0			0				

F = Faint outline of egg visible in radiograph.

In 1995, we attempted to radiograph Espanto female tortoises during the peak windows of ovulation based on 1994 data; June 17 and July 4. The same eight Espanto females studied in 1994 were not gravid in mid-June 1995 and in early July all females except #138 were radiographed, however, a new female # 3 (241mm MCL) was opportunistically captured and X-rayed on that day. Three out of eight females were found gravid in early July; females #108, #3, #120 with six, seven, and five eggs respectively. This suggests that the timing and annual frequency of the reproduction may vary at the site.

Fecundity. Table 11 provides reproductive parameters for the Maricopa and Espanto sites, and for three other localities from the literature. Mean clutch frequency and egg production were dramatically lower for the Maricopa animals compared to other locations. The number of tortoises reproducing was significantly lower at the Maricopa (X^2=6.741, N=13, P<.01) than at the Espanto control site. Otherwise, the range of clutch frequencies (0-1), mean and range of clutch size (5.0; 4-6), were similar between the Maricopa site and the other Arizona sites, and proportional to the Mohave desert sites (see below).

Clutch size generally increases with body size (Fig. 12), as in most animals. However, the regression for the Sonoran Desert is only significant if our data are combined with that of Murray et al. (1996) and an outlier point is excluded. Female 138 (MCL=267 mm) with two eggs in 1994 is the outlier. Adult Maricopa tortoises were generally smaller than Adult Espanto tortoises although tests were not significant for the females studied (rank transformation test, t=1.618, df=13, P=.065). Carapace length correlates positively with clutch size for desert tortoises at the Goffs (Turner et al. 1984; Turner et al. 1986), combined Arizona, and Texas sites in Fig. 13. Fig. 13 suggests that all of these tortoises lie on or near a single size-fecundity regression line.

Body mass. Mass gradually decreased over the reproductive season, undoubtedly due to dehydration during the arid season under study. Table 12 provides the observed mass and recorded rainfall during the reproductive season at the Maricopas. Mass also dropped markedly after oviposition (mean observed decline = 207.2 g). Espanto females were significantly heavier at the onset of ovulation than the Maricopa tortoises based on a comparison of residuals of log mass regressed on log MCL (rank transformation test, t=4.619, df=8, P<.001).

Changes in mass were complicated by tortoises gaining mass after rainfall, although not all tortoises gained mass at that time. There were three precipitation events during the reproductive season averaging 12.7 mm at three locations. Females at Espanto had a mean mass gain of 237.5 g, after a 10 mm rain on 7/17/94.

Soils. Soils were sampled at twelve sites at Espanto Mountain and seven sites at the Maricopa plot (Table 13). On the plot, soils at nest sites contained less gravel than soils from control sites. At Espanto Mountain, soils with low gravel content are more available since it is situated in the valley. There was little difference between soils at nest and control sites at Espanto and although sample sizes are small, some difference was found in gravel content between the nest and control sites on the plot.

Table 11. Comparison of female reproduction parameters at various desert tortoise populations.

Reference	1	1	1	2	2	3	4	4
Site	Goffs, CA.	Goffs,CA.	Goffs, CA.	Yucca Mt, NV.	Yucca Mt, NV.	Mazatzal, AZ.	Maricopa, AZ.	Espanto, AZ.
Year	1983	1984	1985	1993	1994	1993	1994	1994
Number of females studied	19	26	21	9	28	10	6	7
Mean female MCL (mm)	209.1	208.4	215.1		248.2	244.3	242.8	255.9
Range of female MCL (mm)	189-247	189-247	189-246		210-274	220-260	230-257	220-281
Mean clutch fequency	1.9	1.6	1.8	2.0	<2.0	0.8	0.3	1.0
Maximum clutch frequency	3	2	3	2	2	1	1	1
Mean size first clutch	4.1	4.3	4.8			5.7	5.0	5.6
Mean size second clutch	4.2	4.3	5.6			No	Second	Clutch
Mean overall clutch size	4.17	4.28	5.12			5.7	5.0	5.6
Range of clutch sizes	1-7	2-7	3-7	1-7		3-9	4-6	2-9
Mean egg production	7.88	6.72	8.96	8.24	8.46	4.45	1.67	5.57
Nesting period	May-July	May-July	May-July		May-June	June-July	June-July	June-July

1 Turner et al 1986
2 Rakestraw 1994-1995
3 Murray et al. 1995
4 This study

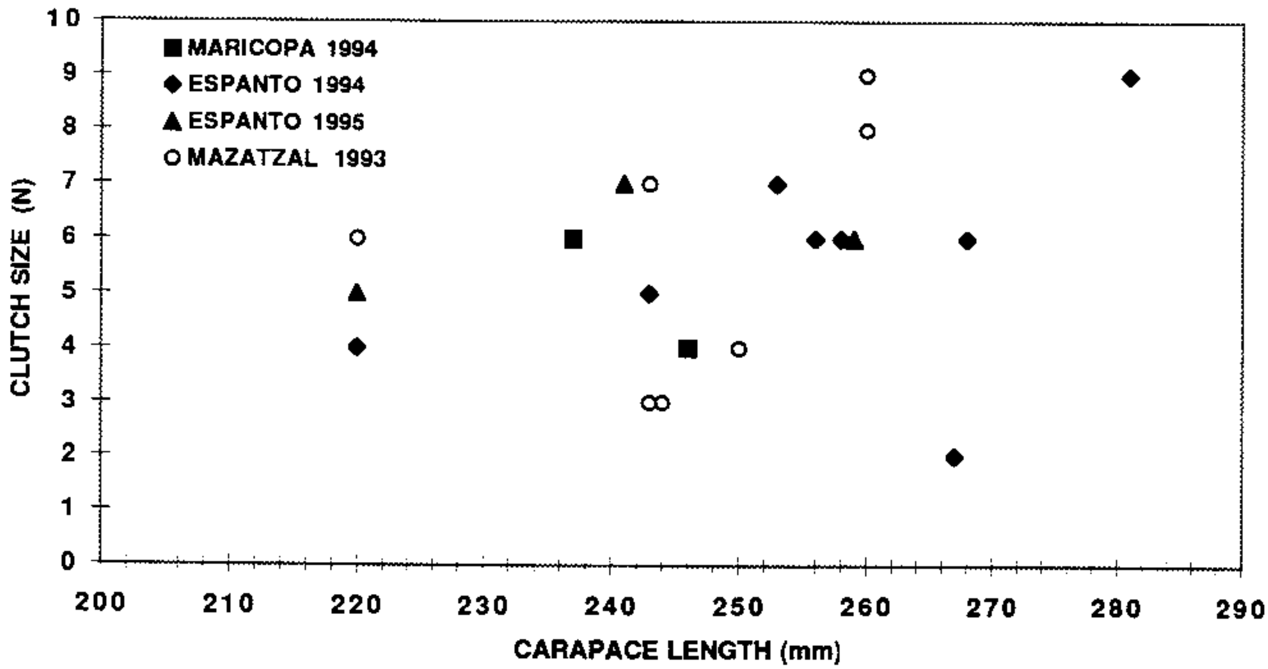

Figure 12. Relationship between clutch size and carapace length from tortoise populations in Arizona. Clutch size = 0.058 X Carapace length - 8.416; r^2=.27, P=.027. The outlying Espanto point, clutch size = 2, is excluded from the regression. Mazatzal data from Murray et al (1995).

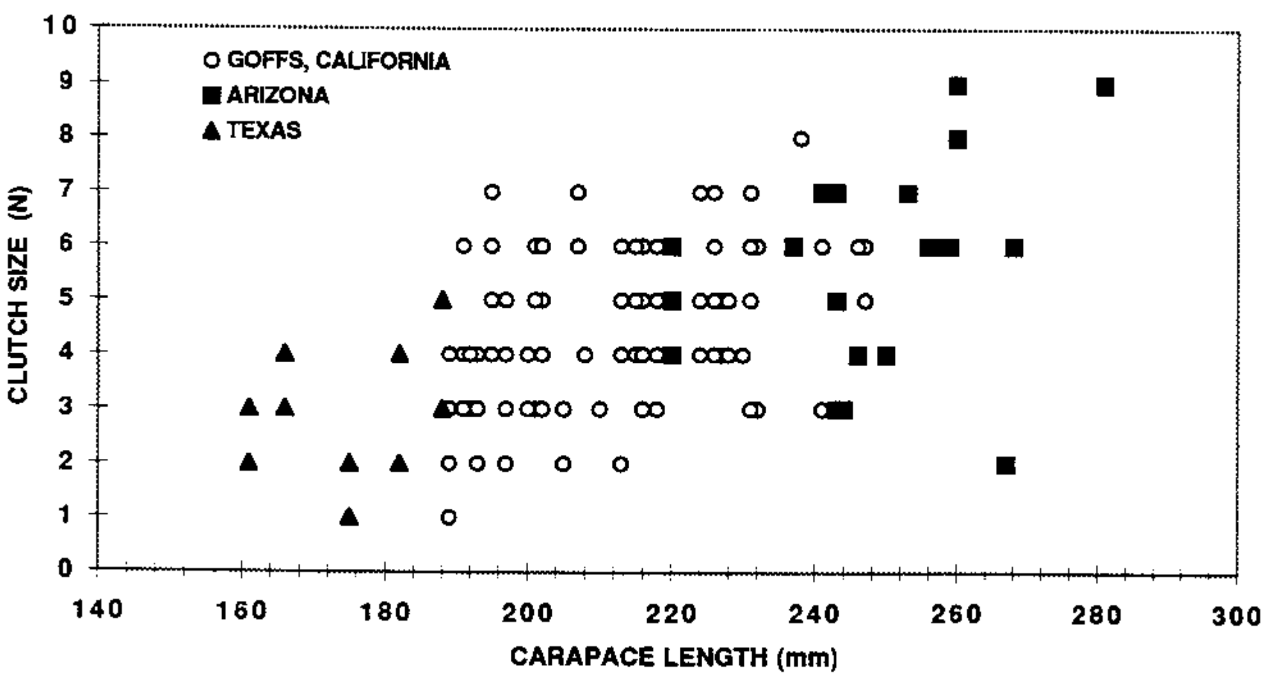

Figure 13. Relationship between clutch size and carapace length from tortoise populations in California (Turner et al 1986), Arizona (Murray et al 1995 and this study), and Texas (Judd and Rose 1989). Clutch size = 0.040 X carapace length - 3.968; r^2=.34, P=8.6E-14. The outlying Arizona point is excluded.

Table 12. Mass (g) for desert tortoises at two sites in the Maricopa Mountains, Maricopa Co., Arizona, 1994. Boxes group weights collected while females were gravid on radiographs. Local precipitation events occured on May 24- 25, June 21, July 18-19, 1994.

ID	11-May	12-May	13-May	22-May	23-May	24-May	5-Jun	6-Jun	12-Jun	17-Jun	21-Jun	22-Jun	28-Jun	1-Jul	3-Jul	8-Jul	13-Jul	19-Jul	23-Jul	24-Jul
Espanto																				
109							4350		4320		4300			3810			3700	3925	3900	
139														3525			2825	3100		
138														3185	3050		3040	3285		
108			2800				2775		2800		2825			2670			2870	2625	2620	
180																		3315	3300	
132							2850		2800		2675			2600			2450	2810	2450	
133							2440		2380	2350	2400			2225			2100	2095	2100	
120			2150	2125					2150		1900			1880			1875	2080		
Plot																				
21	3350				3350					3425			3375			3260				3175
91		2925			2700					2900			2540			2390				
88					2425			2550								2190				
113	2900							2900		2840						2830				2590
63		2400			2390							2410								
101			2150			2125			2140		2100			2100						

Precipitation	May 24-25	June 21	July 18-19
Espanto	6.35mm	T	10mm
Plot	7mm	1mm	1mm
Tort 101	10.41mm	2.3mm	-

Table 13. Soil characteristics at nesting sites for desert tortoises at the Maricopa PSP and at Espanto Mtn., Maricopa Co., Arizona.

Site	Sec./grid	Situation	Texture	% Gravel	Carbonate
Maricopa plot T4S, R2W					
Nest sites:					
1. female 35	19/28	arroyo bank caliche cave	sandy loam	30	yes
2. female 113	18/95	burrow under rock	sandy loam	15	no
3. female 88	18/77	burrow under rock	sandy loam	15	no
Control sites:					
4. veg. transect 11	18/78	N end ridge	sandy loam	40	no
5. veg. transect 12	19/07	W highland side terrace	sandy loam	35	no
6. veg. transect 13	19/38	SW basin alluvium	sandy loam	50	yes
7. veg. transect 14	19/38	SW basin slope	sandy loam	45	some
Espanto Mtn. T4S, R1W					
Nest sites:					
8. female 108 1994	11/69	burrow under rock	sandy loam	15	no
9. female 109 1994	11/63	soil burrow under creosotebush	silty clay loam	2	no
10. female 120 1994	3/89	soil burrow under wolfberry	silt loam	1*	no
				*(+3% macro organic)	
11. female 132 1994	12/82	soil burrow under mesquite	sandy loam	20	no
12. female 133 1994	12/92	under paloverde	sandy clay loam	25	no
13. female 180 1994	11/69	soil burrow under paloverde	sandy loam	15	no
14. unk. female 1994	12/93	adjacent to rock	sandy loam	20	no
15. female 03 1995	13/16	burrow under rock	loamy sand	20	yes
16. female 108 1995	12/80	burrow under rock	sandy loam	40	some
Control sites:					
17.	2/81	NW end at base of slope	sandy clay loam	15	slight
18.	12/70	E side	loam	30	no
19.	13/06	E side	loam	10	no

DISCUSSION

Environmental Conditions and Environmental Correlates

Buckeye PDSI values indicate the 1984-1992 drought did not reach so great an extreme as the 1979-1980 drought, but was the longest in duration for the period for which data are available. It was most severe during the summer months. In duration and seasonal timing, it was unique to the recent history of the Maricopa Mts. Possibly most important, this was a drought caused by extreme heat, coupled with moderately low rainfall.

The sahuaro cactus, a typical Arizona Upland Sonoran Desert plant, was negatively affected during 1987-1995 in the Maricopa Mts. Normal sahuaro mortality rates in Tucson are 1% per year for 3-12 foot high cactus (Betsy Pierson, pers. com.). Sahuaros in the Maricopas died at a 6% higher rate over an eight year period. The mortality rate was highest on S and WSW exposures clearly implicating heat or drought, rather than freezing. Also, we made numerous observations of girdled sahuaro cacti in the Maricopas during the later years of our study: they are apparently girdled during droughts by animals desperately seeking stored moisture in the pulpy flesh (Steenbergh and Lowe 1976). Normally, the spines are adequate protection for the plant, but during droughts animals may risk injury to get at the water.

Observations of other flora and fauna at the Maricopa plot since 1987 also suggest that weather patterns affected organisms besides desert tortoises and sahuaros (see Table 4). It was consistently the species with predominantly eastern distributions and summer rainfall activity maxima that declined during the extended drought, whereas more arid-and heat-adapted species with predominantly western distributions fared better.

Perennial vegetation transects at the Maricopas did not indicate changes over the drought. Perennial vegetation does not respond to drought in a one directional, declining pattern. Long term vegetation studies at Tumamoc Hill in Tucson, AZ (Goldberg and Turner 1986) show that different perennial species responded to a ten year drought differently, increasing, decreasing, or remaining stable. Goldberg and Turner suggest that rarer species respond more dramatically to climatic change, as *Opuntia chlorotica* and *Agave deserti* did in the Maricopas.

Tortoise Mortality Patterns

The 1993 Maricopa PSP census yielded fewer tortoises than in 1990 but the census area was a kilometer instead of a mile. A relatively high mortality apparently did occur in 1991, however, the already diminished population produced far fewer actual shell remains compared to earlier censuses. A surprising number of the 1993 captures were unmarked young males. Subadult survivors may now dominate the population.

Our TSD estimates are based on comparing a continuum of gradual decomposition from shells of individuals marked in 1987 and found dead in 1990 or later, and applying that progression to the unmarked shells. We did not make any estimates past the point of partial articulation. A key for time since death estimates under Mohave Desert conditions (Woodman and Berry 1984) was not used here because the scale has larger time intervals for each subsequent category that does not accommodate estimating absolute numbers of tortoises that died in a given year (<1 yr, 1-2 yrs, 2-4 yrs, >4 yrs). Their study suggests that there is a lot of variation for rates of decomposition, which is undoubtably also true for the Sonoran Desert.

Furthermore, we did not use the Mohave TSD key because our observations indicate a faster rate of decomposition in the Sonoran Desert. When the Mohave key estimates for TSD are applied to the Maricopa tortoise shells (assigned by Peter Woodman) and adjusted to fit, the highest proportion of shells are estimated to have died in 1987. This is unlikely, because we were there in 1987 and did not observe any fresh dead animals among the 65 shell remains found.

Our data show that tortoises may patronize cooler slopes in central and western Arizona. In contrast, Martin (1995) showed that tortoises in the Tortolita Mts., AZ do not favor N and E slopes. While Maricopa tortoises favored the north and eastern slopes, mortality occurred disproportionately on southern and western slopes. This is very strong evidence suggesting a climatic cause (direct or indirect) of the population collapse.

Vegetation is strongly affected by slope aspect. Perennial vegetation transects demonstrated higher structure and diversity on the N and E slopes. The tortoises might have benefitted from a higher quality or diversity diet on the more mesic slopes during the drought. More likely, however, they survived better there because of lower temperatures, and/or the attendant higher residual soil moisture through the drought.

Espanto Mountain did not experience the high tortoise mortality observed in the main Maricopa range. Espanto Mountain is a small rock pile (insulberg) in the valley floor. It is an important yet under-appreciated observation that a valley floor cools off much more at night than does a rocky upland. Anyone who has done much camping in the desert in the summer would surely know this. Espanto Mountain's small mass was able to reradiate heat rapidly into the evening sky and surrounding environment. Further, soils were finer and deeper at Espanto, allowing easier access to less hot and dry refugia than at the PSP. Here, again, we see the tracks of severely hot and dry weather leading to and from the Maricopa tortoise decline.

Adult females had a higher mortality rate than males during the Maricopa drought. Although many shell remains could not be sexed because of deterioration, it is not likely that the sex ratio estimate would be affected. Based on remains observed in the field and estimates of TSD, several tortoises, at least, died during the summer months. The reproduction study showed that females loose a lot of mass after they oviposit their eggs, and are in poor condition until the summer rains begin. If the summer rains were to fail or even be delayed a month, this could be expected to increase female mortality rate, probably accounting for part of the observed differential mortality.

Adult size classes died more than subadults or juveniles. This result may have been biased by the possibility that smaller remains are broken up more quickly than large remains, and therefore may not have turned up in proportion to their actual occurrence. A counterbalancing bias is that young tortoises are also under-represented in the live censuses.

On the avereage , tortoises that died had higher shell domes than those that survived. Because shell shrinkage was a consideration, only marked tortoises that died were compared to tortoises that survived. The height measurement had the highest standard deviation. The Maricopa PSP landscape is primarily boulder strewn and tortoises occupy the spaces under and between boulders. Flatter tortoises may be able to crawl into the deeper microhabitat spaces under boulders. This, together with the observation that intermediate-sized tortoises survived best, suggests that the heat and drought imposed rigorous selection for ability to utilize shelter sites as refugia from the climatic extremes. Over the course of a severe drought, there may be selection favoring flatter shells--a prime character differentiating Sonoran from Mohavean turtles.

Climate, then, was the ultimate cause for the collapse of the Maricopa Mountain PSP tortoise population. Perhaps there were derived, aggravating or secondary factors (e.g. food plants, disease, etc.) although we do not have direct evidence for them. Buckeye PDSI values show that the eight year drought was consistently the worst during summers. Sonoran tortoises in the Tortolita Mts, Arizona have predictable, high activity levels during the summer, but have moderate, variable activity seasons in the spring (Martin 1995). The same observations can be made at the Maricopas and other southern Arizona tortoise localities. This suggests that summer drought or heat might play a large role in Sonoran Desert tortoise population dynamics. However, we can only speculate on the proximate causes of death in the Maricopa decline.

Possible Causes of Mortality

Two physiology dissertations were conducted on desert tortoises in the Mohave Desert during the same years that many of the Maricopa tortoises died (1988 -1990). Peterson (1993) reported that nine (41%) of his Ivanpah, CA study animals died with, "symptoms of dehydration (high plasma osmolality) and/or starvation (high blood urea, as compared to tortoises that survived)". Henen (1994) found that, "lipid-free energy (probably protein) and total body water (TBW) limits egg production and maintenance of body condition". Lipid-free energy is gained from fresh spring annual plants at Goffs, CA (Henen 1994). Both studies commented on drought conditions in 1989 and recorded the physiological effects in their study animals. Desert tortoises tolerate physiological imbalance (high plasma osmolality and high blood urea), much of the year, assuming that conditions will allow balancing fluid concentrations (free water or metabolized water), at least once a year. Desert tortoises at the Maricopas may not have had many opportunities to eat fresh annuals or drink free water. Any that could not regulate plasma osmolality and blood urea levels during a prolonged period within the eight year drought would likely have died.

Henen (1994) states that, "Nonreproductive females may have abandoned egg production because they had smaller TBW and body lipid-free energy reserves". He follows with "reproductive females may have decreased their future chances for survival and reproduction. Female desert tortoises apparently try to produce eggs every year, even drought years". The higher mortality rate of females than males at the Maricopas suggests that reproduction may indeed reduce chances for survival during periods of physiological stress. It also suggests that the onset of physiological stress may have occurred too late to allow females to abandon egg production. Late or inadequate summer rains would have killed a higher proportion of reproductive females at the Maricopas.

Overheating of tortoises was probably a mortality factor at the Maricopas. Zimmermann et al. (1994) found desert tortoises remaining out of their burrows overnight in summer, apparently to reduce body temperature below that obtainable inside the burrows. This enabled them to forage later into the following morning. Such "camping out" behavior has also been observed for tortoises in the Maricopa Mts. However, the boulders at the Maricopa plot absorb and reradiate a tremendous amount of heat. We speculate that "camping out" tortoises would get only a modest cooling, while paying a large price in desiccation in the very warm and dry night time air on the Maricopa slopes. Tortoises in the Maricopas may be trapped between the benefits of leaving burrows to drop body core temperatures at night and the risks of desiccation in the arid night air, literally between a hot rock and a dry place.

Disease has been suggested as an important cause of tortoise mortality. Although we can not rule it out, no disease symptoms were observed among live tortoises in the Maricopas. Peter Woodman (personal communication) has examined the Maricopa shell remains and found high incidence of shell keratinosis, a white flaky material on the plastron. This maybe a symptom of long term environmental stress, but it has not been demonstrated to be lethal, or to be associated with the upper respiratory tract disease that has plagued Mohave desert tortoises in recent years.

Many of the Maricopa shell remains had marks of predators or scavengers (shattered or broken shells, or tooth marks). The mountain lion is known to be able to crush an adult tortoise shell in its mouth, whereas a coyote can snap a plastron with difficulty. Our observations at Organ Pipe Cactus National Monument and AGFD observations at Little Shipp Wash plot suggest that lions can eat several tortoises in a concentrated area. Clearly not all the Maricopa tortoises were killed by lions or coyotes, and lions are equally scavengers and predators; but it remains likely that some of the Maricopa tortoises were killed by mountain lions or other predators.

Tortoise diets at the Maricopas show that perennials were the primary food, including woody trees and shrubs. Comparisons with other available Southern Arizona tortoise data suggest the Maricopa tortoises diet was higher in perennials than might normally be expected. Henen (1994) argues that ephemerals are nutritionally important in tortoise diets. This suggests that dietary stress may have existed in the Maricopas, and may have been a contributing factor in the mortality

Reproduction

Oviposition dates. The Maricopa tortoises were reproductive in June and July. However, a broad time window is still needed to study reproduction in desert tortoises to accommodate year to year variation and possible, infrequent multiple clutches although multiple clutching is not known in the Sonoran Desert. The challenge of studying wild Sonoran desert tortoise reproduction is successfully extracting the tortoises from their burrows on a regular basis. This feat has continued to prevent researchers from determining how much variation there is in timing of ovulation and oviposition. The ovarian cycle may be determined by climatic conditions causing tortoises within the same deme to ovulate more or less synchronously within any given year, as the 1995 data suggest. Sexual differences in tortoise hibernation (Bailey et al. 1995) are likely connected to sexual differences in reproductive cycles, and related to the timing of ovulation. Clearly, additional, and also more extensive, reproductive studies are needed.

Clutch frequency. The reproductive output for desert tortoises at the Maricopa population was clearly lower than at Espanto, due to the lower proportion of females producing. We believe this is correlated with the stress factor(s) that caused the mortality and population crash. Other than this, the range of clutch frequencies, and mean and range of clutch size, are similar among the Maricopa sites and those elsewhere in Arizona. Sonoran desert tortoises may be unable to produce multiple clutches per year because they simply do not have the resources. Mohave tortoises produce 2-3 times the number of eggs per year due to higher clutch frequency.

Clutch size. Carapace length correlates positively with clutch size for desert tortoises at the Goffs, Mazatzals, Espanto, and Maricopa sites. Adult females at the Maricopas were expected to produce smaller clutches because they were smaller-bodied than Espanto tortoises. If some minimum clutch size is fixed in the life history, even though modulated by body size, Sonoran desert tortoises may produce eggs in an "all or nothing" effort depending on body condition. Female 138 had an MCL of 261mm and a clutch size of two in 1994 . Either she really had an unusually small clutch for her size or she had already deposited part of her clutch prior to capture.

Body mass. Body mass is difficult to interpret because tortoises have a large water storage bladder and can increase their mass dramatically by drinking after a single rainfall event. Changes in mass are not an adequate means of estimating reproductive status. The Maricopa tortoise mass measurements are best interpreted for overall trends. Maricopa females started the reproductive season lighter than Espanto females, which correlates with poor condition, and that very likely led directly to the low number of females reproducing. Body mass gradually dropped over the reproductive season for all females. This coincided with hot dry weather, so mass loss is presumed to be primarily dehydration. Still, the largest drop in mass occurred after oviposition. Tortoises continued to gradually loose mass until the rainy season. This suggests that tortoises should, optimally, be at high mass condition at the onset of reproduction. They may face risks of mortality or long term deterioration of health under the stress of mass loss in the foresummer drought, followed by the additional water loss associated with egg production and deposition. This may mean that Sonoran desert tortoise females should, optimally, enter hibernation in excellent condition, since spring conditions and foraging activity is variable. The period between emergence from hibernation and ovulation (as the foresummer drought becomes harsh) is a key opportunity for females to "top off" their condition in advance. This may explain the shallower hibernation and earlier, more extensive spring emergence and foraging in females compared to males (Bailey et al. 1995). Inability of the tortoises to accomplish this "top off" properly during the drought may have contributed both to poor reproduction and to the higher mortality found in females compared to males.

Nest Soil. Nest soils at the Maricopas showed a slightly higher gravel content than at Espanto. The data set is small, but nonetheless suggests that tortoises may be selecting loam soils with moderate to low gravel and rock content for nesting. The relationship between desert tortoises and soil may not be related exclusively to the type of soil, but also, or especially, to the amounts of soil available in the habitat. It is quite possible that the larger quantity of soil available in the valley floor is what aided the Espanto tortoises in surviving the Maricopa drought, because soil maintains moisture and humidity longer than gravel does.

Mortality, Environment, and Reproduction

This section attempts to summarize our findings according to an annual cycle to show how the timing of events contributed to the mortality. The typical Sonoran desert tortoise yearly cycle accommodates a bimodal rainfall distribution. The Sonoran desert is characterized as having winter and summer rainfall seasons, and there are two pulses of tortoise activity, spring and summer.

Winter rainfall in the Sonoran Desert is variable and is unpredictably spread over a long season (Oct. or Dec. through Feb. or April). Thus spring can range from very moist to extremely dry. Sonoran desert tortoises have responded with a variable spring activity season. Male and female tortoises hibernate at different temperature regimes; females hibernate at shallow depths and males more deeply (Bailey et al. 1995). Females experience wide temperature fluctuations because they are closer to the surface, and they often emerge earlier in the spring to feed on spring ephemerals. Most likely this enables them to improve their body condition before ovulation. Spring ephemeral wild flower displays are highly variable, and tortoises may not benefit every year. During dry springs, both sexes may remain in hibernation later into the spring (Wirt pers. obs.). In the Maricopas during the population decline and during our reproduction study, females probably did not gain much mass, because spring drought prevailed. Females presumably also dehydrated during winter while in shallow hibernacula.

During late spring, females become gravid more or less synchronously. They continue to feed, but have low to moderate activity due to the hot arid nature of the season. At this time they minimize evaporative water loss by residing in soil burrows or deep cool rock shelters. Oviposition occurs just before the summer rains, leaving the females in very poor condition. Under these protracted drought conditions, reproductive investment by females would be expected to increase their mortality rate, consistent with our observations.

Sonoran desert tortoises become increasingly active in mid-late July with or without the first summer rains (Martin 1995). Eventually, perennial grasses and summer ephemerals flush out, and a second wave of summer rainfall is a common occurrence during the hurricane season in early September. Tortoises are in their full glory; feeding, mating, defending territory, and putting on mass as late into the fall as conditions permit. Shortened days and unexpected cold snaps in the fall appear to force tortoises back into hibernation.

During the Maricopa drought, summer rains sometimes began in late August or early September, and there were often long periods between significant rainfall events. The increased tortoise activity starting in July may have expended dwindling water and lipid reserves in both sexes. Males may have diverted lipid reserves toward spermiogenesis and toward making large movements throughout their home range in search of mates. Females were in poor condition from oviposition; their losses may have been cut because they often remained in burrows defending their nests (Murray et al. 1996). Both sexes probably have re-established water balance by late summer, but they may have gained little fat for hibernation or reproduction.

More of the remains were females and more remains were adults rather than subadults. Adults, especially females, may have been unable to recoup reproductive energy investments.

All tortoises fed more heavily on perennials than ephemerals, because ephemerals were less available. Henen (1994) found that ephemerals provide superior forage for lipid storage; the Maricopa tortoises were apparently forced to feed primarily on lower quality food. Hailey and Loumbourdis (1988) found lipids stored in follicles and speculated that due to the herbivorous nature of tortoises, lipid storage buildup is a long-term process.

Once or twice a decade, spring ephemerals occur in remarkably high densities. These are the years we see displayed in calendars depicting desert wild flower blooms. Such a bloom occurred in the Maricopas in spring 1995; male and female tortoises emerged from hibernation in late February and grazed heavily all spring. This may be a similar scenario to the one that Paul Schneider found in 1980: He remarked that March and April must be peak activity months for Sonoran desert tortoises (Schneider 1981). The 1995 spring activity did not translate directly into enhanced reproductive output that summer. Rather, such feeding windfalls are probably important in long term energy balance, extending over a period greater than a season or a year, for the adult Sonoran desert tortoise.

During much of the drought, ambient temperature remained high and soil moisture low; cool burrows may have become a critical resource for the Maricopa tortoises. Many of the shell remains had high domes or were of large tortoises. These individuals may have had difficulty retreating deeply enough under boulders to cool, moist microhabitats. As meager summer rains turned into dry falls, tortoises retreated into hibernation early (Shields et al. 1990) because so little could be gained by foraging. The activity season was shortened by nearly a month, and fat buildup was almost surely restricted. Over an eight year drought, this scenario may have been almost chronic, contributing to the stress experiences by the Maricopa desert tortoises. In short, we suggest that the heat and aridity of the drought produced a syndrome of ecological stresses that led to the death of most of the tortoises alive in the mid-1980s population.

CONCLUSIONS AND RECOMMENDATIONS

The desert tortoise population in the Maricopa Mountains will gradually recover, provided climatic patterns return to a more moderate balance, as demonstrated in the Buckeye PDSI graph from 1950 to 1978 (Figure 4). Whether or not the erratic climatic pattern shown in 1979 to 1992 was a result global climate change cannot be stated definitely at this point. Population recovery would necessarily be slow since few females remain at the Maricopas, and reproductive rates are slow. Further research on reproduction of Sonoran desert tortoises is needed to understand why all females were not reproductive at the Maricopas and Mazatzals. Many unresolved issues remain. We identify the following key areas for further study and evaluation based on our findings and the exploratory discussion we have provided herein:

1. Since climate change is a plausible (cause?) scenario for the heat wave enveloping Arizona over the past decade, researchers and field personnel should become conscious of the possibility that tortoises, and other organisms, may begin to show unusually strong effects of heat and associated drought stress.

2. Research on and monitoring of desert tortoises in the Southwest needs to be expanded to include key aspects of the ecology that may be in control of body condition, reproductive output,

and survivorship. These appear to be the key facets of the population decline in the Maricopa Mountains. Current efforts are very strong in standardized population monitoring. In general, we suggest that it is time to enhance these efforts by engaging in properly directed ecological study, especially where this is possible in tandem with the established protocols. We suggest the following:

A. Long term reproductive studies must be continued and carried out in additional areas, with intent to compare data.

B. Greater depth should be added to the reproductive studies, especially regarding individual female behavior, nest sites, and natural mortality (including predation) of nests. Another key area of understanding is related to lipid storage, the time-scale involved in individual body condition, and the relationship of diet and drinking to body condition.

C. Further study of recruitment--especially the relationship of juveniles and subadults to climatic factors--is indicated by our results. A goal should be to construct life tables for Arizona tortoise populations.

D. Systematic study of mortality is needed to pin down the proximate causes of death. This will require regular survey of established study areas with an attempt to recover remains soon enough to assist establishing individual causes of death.

E. Careful and thoughtful climate and micro-climate monitoring of selected tortoise habitat areas is indicated. We need to understand the distribution and availability of retreats of various sizes and qualities, especially in relationship to the number of turtles vying for the resource. Specifically, we need to examine the operative environment (temperature, moisture, humidity, food) of the desert tortoise in the Sonoran Desert.

A careful evaluation should be made in deciding where to focus plot census operations, so that data most pertinent to questions of population process will accumulate in a timely manner.

3. Field personnel should become educated about the need to collect key information on remains of tortoises encountered by chance during ongoing work of various kinds. When fresh remains are found, they should be collected, and careful notes attached concerning locality, date, observer, and position of the remains in the habitat, especially slope, aspect, general vegetation, and proximity to cover in the form of burrows, crevices, and vegetation.

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Appendix I. Relative frequencies of annual plant species found in 79 desert tortoise scat samples compared to relative frequencies among eight vegetation quadrats at the Maricopa PSP, Maricopa Co., Arizona.

		Diet analysis		Vegetation analysis	
Form	Species	Freq. N	Rel. Freq %	Freq. N	Rel. Freq. %
ephemeral	*Eucrypta chrysanthemifolia*	19	10.33	0	0.00
ephemeral	*Lepidium lasiocarpum*	16	8.70	0	0.00
ephemeral	*Plantago insularis*	14	7.61	7	13.73
ephemeral	*Boerhaavia intermedia*	10	5.43	0	0.00
ephemeral	*Bromus rubens*	10	5.43	4	7.84
ephemeral	*Daucus pusillus*	9	4.89	2	3.92
forb	*Euphorbia micromera*	9	4.89	0	0.00
grass	Indet. grasses	8	4.35	0	0.00
forb	*Euphorbia abramsiana*	7	3.80	0	0.00
ephemeral	*Pectocarya recurvata*	7	3.80	2	3.92
forb	*Euphorbia (Chamaesyce)* sp.	6	3.26	0	0.00
ephemeral	*Phacelia distans*	5	2.72	0	0.00
ephemeral	*Bowlesia incana*	4	2.17	0	0.00
ephemeral	*Gilia* sp.	4	2.17	0	0.00
ephemeral	*Lotus saluginosus*	4	2.17	3	5.88
grass	*Muhlenbergia microsperma*	4	2.17	0	0.00
ephemeral	*Boerhaavia wrightii*	3	1.63	0	0.00
ephemeral	*Calandrina ciliata*	3	1.63	1	1.96
ephemeral	*Cryptantha barbigera*	3	1.63	0	0.00
grass	*Erioneuron pulchellum*	3	1.63	0	0.00
ephemeral	*Erodium cicutarium*	3	1.63	1	1.96
ephemeral	*Lotus strigosus*	3	1.63	0	0.00
ephemeral	*Phacelia crenulata*	3	1.63	0	0.00
forb	*Astragalus* sp.	2	1.09	1	1.96
ephemeral	*Boerhaavia erecta*	2	1.09	0	0.00
ephemeral	*Boerhaavia* sp.	2	1.09	0	0.00
ephemeral	*Chorizanthe brevicornu*	2	1.09	0	0.00
ephemeral	*Cryptantha* sp.	2	1.09	1	1.96
forb	*Euphorbia melanadenia*	2	1.09	0	0.00
forb	*Euphorbia pediculifera*	2	1.09	0	0.00
grass	*Bouteloua barbata*	2	1.09	0	0.00
ephemeral	*Amsinkia intermedia*	1	0.54	0	0.00
ephemeral	*Amsinkia tesselata*	1	0.54	0	0.00
ephemeral	*Boerhaavia coulteri*	1	0.54	0	0.00
ephemeral	*Cryptantha decipiens*	1	0.54	0	0.00
ephemeral	*Cryptantha maritima*	1	0.54	0	0.00
ephemeral	*Dyssodia concinna*	1	0.54	1	1.96
ephemeral	*Eschscholtzia* sp.	1	0.54	0	0.00
ephemeral	*Lupinus sparsifloris*	1	0.54	2	3.92
ephemeral	*Perityle emoryi*	1	0.54	0	0.00
ephemeral	*Thysanocarpus curvipes*	1	0.54	0	0.00
ephemeral	*Tidestromia lanuginosa*	1	0.54	0	0.00
ephemeral	*Cryptantha pterocarya*	0	0.00	0	0.00
ephemeral	*Eriophyllum lanosum*	0	0.00	2	3.92
ephemeral	*Schismus barbatus*	0	0.00	3	5.88
	UNK	0		17	
	TOTALS	184		47	

Appendix II. Relative frequencies of perennial plant species found in 79 desert tortoise scat samples compared to relative frequencies among 14 vegetation transects and quadrats at the Maricopa PSP, Maricopa Co., Arizona.

		Diet analysis		Vegetation analysis		Preference
Form	Species	Freq. N	Rel. Freq. %	Freq. N	Rel. Freq. %	
shrub	*Janusia gracilis*	34	15.74	6	4.20	11.54
shrub	*Eriogonum fasciculatum*	25	11.57	8	5.59	5.98
shrub	*Sphaeralcea ambigua*	24	11.11	8	5.59	5.52
tree	*Cercidium microphyllum*	29	13.43	12	8.39	5.03
forb	*Dyssodia porophylloides*	11	5.09	1	0.70	4.39
tree	*Olneya tesota*	11	5.09	3	2.10	2.99
shrub	*Ditaxis* spp.	11	5.09	5	3.50	1.60
shrub	*Crossosoma bigelovii*	3	1.39	0	0.00	1.39
shrub	*Agave deserti*	2	0.93	0	0.00	0.93
forb	*Eriogonum wrightii*	2	0.93	0	0.00	0.93
shrub	*Hibiscus denudatus*	2	0.93	0	0.00	0.93
shrub	*Acacia constricta*	1	0.46	0	0.00	0.46
forb	*Allionia incarnata*	1	0.46	0	0.00	0.46
shrub	*Ayenia* spp.	1	0.46	0	0.00	0.46
forb	*Eriogonum sp.*	1	0.46	0	0.00	0.46
forb	*Eriogonum tricopes*	1	0.46	0	0.00	0.46
forb	*Marina parryi*	1	0.46	0	0.00	0.46
forb	*Mirabilis bigelovii*	1	0.46	0	0.00	0.46
shrub	*Porophyllum gracile*	1	0.46	0	0.00	0.46
forb	*Ameranthus fimbriatus*	2	0.93	1	0.70	0.23
shrub	*Hyptis emoryi*	6	2.78	4	2.80	-0.02
shrub	*Acacia greggii*	1	0.46	1	0.70	-0.24
cactus	*Opuntia* spp.	7	3.24	5	3.50	-0.26
cactus	*Carnegia gigantea*	5	2.31	4	2.80	-0.48
grass	*Aristida purpurea*	0	0.00	1	0.70	-0.70
cactus	*Echinocactus engelmannii*	0	0.00	1	0.70	-0.70
grass	*Muhlenbergia porteri*	0	0.00	1	0.70	-0.70
shrub	*Zizyphus obtusifolia*	0	0.00	1	0.70	-0.70
forb	*Dalea mollis*	1	0.46	2	1.40	-0.94
forb	*Euphorbia eriantha*	0	0.00	2	1.40	-1.40
forb	*Fagonia californica*	0	0.00	2	1.40	-1.40
shrub	*Lotus rigidus*	0	0.00	2	1.40	-1.40
shrub	*Macheranthera pinnatifida*	0	0.00	2	1.40	-1.40
shrub	*Larrea divaricata*	6	2.78	6	4.20	-1.42
shrub	Compositae	1	0.46	3	2.10	-1.63
shrub	*Galium stellatum*	1	0.46	3	2.10	-1.63
shrub	*Krameria (cf K. grayi)*	3	1.39	5	3.50	-2.11
shrub	*Ephedra (cf E. aspera)*	1	0.46	4	2.80	-2.33
shrub	*Lycium berlandieri*	8	3.70	9	6.29	-2.59
shrub	*Menadora scabra*	0	0.00	4	2.80	-2.80
shrub	*Fouqueria splendens*	3	1.39	6	4.20	-2.81
shrub	*Viguieria deltoidea*	0	0.00	5	3.50	-3.50
shrub	*Sapium biolculare*	3	1.39	8	5.59	-4.21
shrub	*Encelia farinosa*	4	1.85	9	6.29	-4.44
shrub	*Ambrosia deltoidea*	2	0.93	9	6.29	-5.37
	TOTALS	216		143		

forb	moss	1	0.46
forb	*Selaginella arizonae*	6	2.75
forb	ferns (incl. *Notholaena*)	6	2.75
	TOTALS	218	